Selection for Stem Rust Resistance in Tall Fescue and Its Correlated Response with Seed Yield

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ABSTRACT

Genetic resistance to stem rust (caused by *Puccinia graminis* Pers.:Pers. subsp. *graminicola* Z. Urban) could reduce the need for fungicides to control the disease in tall fescue [*Lolium arundinaceum* (Schreb.) Darbysh. (=*Festuca arundinacea* subsp. *arundinacea*)] grown for seed. Two populations from 14 resistant forage-type plants (F) and 20 turf-types (T) were developed using polycross (PX) and open pollination (OP) progenies. A two-stage controlled environment inoculation was used for screening and selection for two cycles. Direct selection response was determined after two artificial inoculations in a controlled environment. Indirect selection response for seed yield was measured, using the same plants as the direct selection study, in the field using natural inoculation for 4 yr. Plants with resistant reaction, based on pustule type, increased from 5 to 54% in the F population and from 6 to 50% in the T after two cycles of PX selection and from 5 to 63%, and from 6 to 50% in the F and T populations, respectively, after one cycle of OP followed by one cycle of PX selection. In each selection scheme, the largest increase came from the first PX cycle. Seed yield of tall fescue with improved stem rust resistance was higher than for susceptible populations or cultivars with heavy stem rust presence (1998), but yields were similar with no rust pressure (1999). These results indicate that seed yields in tall fescue can be maintained using genetic resistance to stem rust sufficient to slow or eliminate disease epidemic development.

TALL FESCUE is used for both forage and turf in temperate regions of the world. More than 60 000 ha of tall fescue are grown for seed in Oregon and it ranks second in hectarage among grasses grown for seed in the Willamette Valley of Oregon (Young, 2001). Stem rust was first reported in tall fescue seed production fields in Oregon in 1987 (Welty and Mellbye, 1989), and the economic impact of the disease has increased in recent years. Fungicides are commonly used to control the disease in grass seed production (Pscheidt, 1996). Genetic host resistance to the disease, however, would provide a more environmentally sound approach for control. Incorporation of host resistance has been successful in controlling rusts of wheat (*Triticum aestivum* L.; Dyck and Kerber, 1985), barley (*Hordeum vulgare* L.; Cotter and Levine, 1932), and maize (*Zea mays* L.; Hooker, 1985).

While genetic host resistance to stem rust in tall fescue had not been reported prior to our studies, it had been found in Kentucky bluegrass (*Poa pratensis* L.; Britton and Butler, 1965; Elliott, 1963; Johnson-Cicalese et al., 1983; Pfleger, 1973; Rogerson and King, 1954; Watkins et al., 1981) and timothy (*Phleum pratense* L.; Braverman, 1966; Nielson and Dickson, 1958). In addition, several cultivars of perennial ryegrass (*Lolium perenne* L.) with reduced susceptibility to stem rust, developed through selection in the field after natural inoculation, have been released (Robinson et al., 1988; Meyer et al., 1989; Meyer and Rose-Fricker, 1990). These cultivars, however, rapidly lost resistance as generations of seed production increased most likely because there was insufficient number of plants with resistance in base populations or the field screening technique was not adequate, and because the host-pathogen interaction for ryegrass is poorly understood.

Welty and Barker (1993) surveyed 20 cultivars of tall fescue for resistance to stem rust. Overall, none of the cultivars per se were judged resistant, but some cultivars had plants with a resistant reaction from both artificial inoculation in the greenhouse and natural inoculation in the field. The resistant plants were saved and used as the base populations in a selection program to improve stem rust resistance. This study reports the direct selection responses from two cycles of recurrent selection in controlled environment screening and the indirect responses on seed yield of tall fescue when grown for four years in the field.

MATERIALS AND METHODS

Source plants for this study were selected from among 1400 plants in a nursery established in 1990 containing 70 plants from each of 20 cultivars (Welty and Barker, 1993). Selection criterion, as described by Welty and Barker (1993), was freedom from stem rust symptoms after two inoculations on seedlings in a controlled environment chamber and two scoring periods (July 11 and 23) in 1990 after plants were transplanted to the field. Thirty-four plants had resistant reactions in controlled environment inoculations and were scored as resistant in field plots. These plants were divided into two populations based on the intended use of the cultivar from which they came. Twenty plants were placed in a turf-type population (T) with plants coming from the cultivars Arid (6), Mesa (6), Thoroughbred (4), Finelawn I (2), Finelawn 5GL (1), and Adventure (1); fourteen plants in a forage-type population (F) coming from the cultivars Kentucky 31 (10) and Forager (3); and one plant from 'Johnstone', a tall fescue backcross derivative from an annual ryegrass (*Lolium multiflorum* Lam.) × tall fescue hybrid.

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Abbreviations: AIT, average infection type; C1, cycle 1; C2, cycle 2; source population; F, forage-type population; PX, polycross; OP, open pollinated selection; OP-PXr, OP followed by PX selection for resistance; OP-PXs, OP followed by PX selection for susceptibility; SSE, super susceptible check; T, turf-type population.

Population Development

The T and F populations were developed simultaneously through two selection cycles as described by Barker and Welty (1996). Open pollinated seed, developed by pollination from either resistant or susceptible plants, of the 34 original plants was harvested by maternal parent. Equal quantities of seed were composited within the F and T populations and designated OP C1. Ten ramets were also collected from each original plant and established in PX blocks isolated by distance or cereal rye (*Secale cereale* L.) borders.

Following an establishment year in the PX nurseries, seed from each ramet was harvested, hand-threshed, and conditioned using hand screens and a commercial laboratory seed blower. Equal quantities of seed from each ramet was composited by maternal parent, designated PX C1, and stored in a cool (5°C), dry room until needed for the next selection cycle, or for selection progress testing.

For the second selection cycle (C2), OP and PX seeds from both the F and T populations were germinated and sixty seedlings from each maternal line were transplanted to 4.0- by 19.5-cm plastic cone pots (conetainers) filled with commercial potting soil mix. Seedlings were screened in the same greenhouse test through two inoculations with stem rust urediniospores using the conditions, urediniospore concentrations, and procedures of Welty and Barker (1993). Disease infection type was scored by pustule type on each plant with 0 = no macroscopic sign of infection and 4 = large uredinia and abundant sporulation. This second cycle was among and within family selection on both OP and PX progenies, but designated as a PX cycle. Maternal families with the lowest AIT score within populations were identified and individual plants within the selected families were chosen based on freedom from any stem rust symptoms in both inoculations. Three plants were saved from each of seven families for the T populations and from five families for the F populations. Bidirectional selection was done on the OP groups to provide second cycle seedlings for susceptibility to stem rust as well as those with resistant reactions. Selected plants for all populations were divided into 10 ramets each and established in six separate isolated PX blocks in the field. Seed was produced as described for C1.

Direct Selection Response

Selection progress from two cycles of PX selection and one cycle of OP selection followed by one cycle of among and within-family (PX) bidirectional selection for resistance or susceptibility (OP-PXr and OP-PXs) for the F and T populations was evaluated in a greenhouse test. Equal quantities of seed from each plant in the isolated crossing blocks was composited by maternal family to form the populations that were used in tests to determine response from selection. The C0 populations were composite seed of the cultivars from which the F and T populations were derived. Six commercial cultivars, Arid, Bonanza, Forager, Kentucky 31, Mesa, and Thoroughbred were included as check populations in the selection progress tests. Five of the cultivars were the same seed sources that provided the original resistant plants. A *super susceptible* check (SSE), developed from PX seed of six highly susceptible plants from 'Orino' (3) and one each from 'Mojave' and two tall fescue experimental populations, was also included.

Selection progress was measured on 10 plants in each of 12 replications (120 total plants for each cycle, population, and check cultivar) and was tested by the two-stage inoculation procedure in a controlled environment chamber. Disease infection type was scored as described above (Welty and Barker, 1993). Average infection type (AIT) was computed for each entry and the frequency (%) of individual plants with a resistant reaction (0 or 1 score in both inoculations) was determined. Realized gain was calculated as the difference in frequency of plants with resistant reaction between two successive selection cycles, for example, $\Delta G = C1 - C0$.

Indirect Selection Response on Seed Yield

Identity of individual plants was maintained from the direct selection response study and they were transplanted to a field near Corvallis, OR (44°38′ N, 123°12′ W), to measure indirect response on seed production. Plants in the field were arranged in four replications of 20 plants each with 10 plants coming from each of two reps in the direct selection response study to one rep in the field. Plots consisted of two rows of 10 plants each spaced on 30-cm centers within rows, and rows spaced 0.5 m apart. Plots were spaced 1 m apart. The soil type was a Woodburn silt loam (fine-silty, mixed, superactive, mesic Aquultic Argixerolls) on 0 to 3% slopes. The plot area was fertilized by soil incorporation of 35.8 kg N ha^{-1}, 15.4 kg P ha^{-1}, 29.7 kg K ha^{-1}, and 15.7 kg S ha^{-1} applied as a complete blend prior to transplanting in 1995. Thereafter, fertilizer was applied in split applications: 33.1 kg N ha^{-1}, 17.8 kg P ha^{-1}, and 31.1 kg S ha^{-1} as a blend of ammonium phosphate (16-20-0, N-P-K) and ammonium sulfate (20-0-0-24, N-P-K-S) in fall (mid-November 1995, 1996, 1997, and 1998) and two applications of 61.6 kg N ha^{-1} as urea in spring (early March and mid-April 1996, 1997, 1998, and 1999). Irrigation was applied immediately after transplanting and at short intervals thereafter in 1995 for establishment. Irrigation was not applied after 1995. Weeds were controlled with applications of 0.28 kg a.i. ha^{-1} of bromoxynil (3,5-dibromo-4-hydroxybenzonitrile) plus 0.28 kg a.i. ha^{-1} MCPA [(4-chloro-2-methylphenoxy) acetic acid] after emergence and 2.24 kg a.i. ha^{-1} of diuron [N′-(3,4 dicholorophenyl)-N,N-dimethylurea] each fall. Alleys between plot ranges were 8 m wide and maintained as bare soil throughout the experiment and were kept weed-free by hand, mechanical cultivation, and spot application of glyphosate [N-(phosphonomethyl)glycine] as needed.

Seed was harvested on a plot basis by maturity of each entry when inflorescences were at ≈43% moisture (Klein and Harmond, 1971). Harvested biomass was placed in jute bags and hung from wire lines to air dry in the field, then threshed in a horizontal-belt thresher. Seed was cleaned through a seed scalper to remove excess straw and final cleaning was done with two passes through an M2B (Crippen International, Dallas, TX) seed cleaner. Seed yield was calculated from weight of total clean seed. Counting 1000 seeds through an electronic counter and weighing determined individual seed weight. Seed yield data were collected in 1996, 1997, 1998, and 1999.

Stem rust in field plantings was scored in 1997, 1998, and 1999 after anthesis on an individual plant basis and averaged for each plot. A severity score (0 to 4 = worst) was based on pustule type and estimated percentage leaf area diseased (see footnote Table 3), and incidence was the percentage of plants in a plot infected with rust.

Data were analyzed using the General Linear Models (GLM) procedure (SAS Institute, 1989) to conduct an analysis of variance (ANOVA) as a split-plot in time across 4 yr (Snedecor and Cochran, 1980). Mean separations were by *t* tests using the LSMEANS option of GLM. All effects except replications were considered random in the statistical model.

RESULTS AND DISCUSSION

Direct Selection Response

Plants receiving pustule type scores of 0 or 1 were considered to have a stem rust resistant reaction, and

those with scores of 2, 3, or 4 were susceptible. Number of plants with resistant reaction in both inoculations increased from 5% (AIT = 3.1) to 54% (AIT = 1.1) in the PX F population and from 6% (AIT = 3) to 50% (AIT = 1.1) in the PX T population (Table 1). The first cycle of PX selection produced 73 and 89% of the realized gain as determined by frequency of resistant plants in the F and T populations, respectively. Final response from OP followed by PX selection (OP-PXr) was similar to PX selection alone, however 78 and 50% of the realized gain for the F and T populations, respectively, was achieved in the PX cycle within initial OP plants. Phenotypic variance of AIT increased with one cycle of selection in both populations, but decreased in C2 (the PX cycle) of the OP plants. Reverse selection for susceptibility (OP-PXs) for only one cycle resulted in fewer resistant plants than in C0 and phenotypic variance for AIT also decreased (Table 1). The increased frequency of susceptibility indicates how rapidly realized gains could be lost in OP field screening tests utilizing natural populations of the rust pathogen if resistant plants could not be recognized because of low stem rust pressure. Commercial breeders often practice OP selection for stem rust resistance because onset of stem rust in the field is commonly apparent only after pollination, and this practice is a common cause for slow genetic gains.

Results indicated that rapid progress from controlled inoculation selection for stem rust resistance in tall fescue is possible if both male and female parents have resistance. Rapid response from one cycle of PX selection indicated few major genes may be involved in stem rust resistance in tall fescue. One cycle of OP selection, with pollen from either susceptible or resistant plants, produced half the gain of PX selection as theory would predict, but when OP was followed by a PX cycle, similar end results to two cycles of PX selection was found. Welty and Barker (1993) demonstrated that resistance detected in the greenhouse is maintained under field conditions. Hence, it is more important to control the pollen parent by selecting at the seedling growth stage under controlled inoculation conditions than to select mature plants in the field without inoculation control.

Frequency of plants with resistant reaction in both inoculations ranged from 0 to 11% and AIT from 2.9 to 3.7 for check cultivars included in the direct response test (Table 2). All cultivars tested in this and other studies using the controlled environment inoculation procedure were classified as susceptible and had <11% plants that were judged resistant (data not shown).

Table 2. Frequency of individual plants with stem rust resistant reaction (R) in both of two inoculations and average infection type (AIT) for tall fescue check cultivars.

Cultivar	R† plants	AIT score‡
	%	
Kentucky 31	11	2.9
Arid	8	3.1
Mesa	5	3.0
Thoroughbred	4	3.3
Bonanza	2	3.3
Forager	2	3.4
SSE§	0	3.7
LSD0.05		0.3

† Resistant reaction (R) to stem rust was determined for an individual plant by receiving a pustule type score of 0 or 1.
‡ Pustule type scores were on a 0 to 4 scale as follows: 0 = no uredinia or visible symptoms, 1 = small uredinia with necrotic edge, 2 = small to medium uredinia with limited urediospore production, 3 = medium-sized uredinia with moderate sporulation, 4 = large, ragged uredinia with abundant sporulation.
§ SSE = super susceptible check.

SEED YIELD RESPONSE

The effects for variety/selection cycle, years, and variety/selection cycle × years were highly significant ($P < 0.0001$) in the ANOVA for seed production traits and reaction to stem rust infection. These three sources of variation made up 60% or more of the total variation in the statistical model.

Response to selection for stem rust resistance, as measured by severity and incidence after natural inoculation in the field, followed closely the direct selection response pattern of number of resistant plants after controlled inoculation (Table 3). Lower severity scores and incidence were obtained after one cycle of PX selection (C1 in the PX group and C2 in the OP group). Response was similar for both the F and T populations. Decrease of incidence, or increase in frequency of resistant plants, will increase overall cultivar response to stem rust infection. It may not be desirable, however, to have 100% resistant plants because this would put high selection pressure on the pathogen to overcome host resistance. A frequency of resistant plants >50% could delay epi-

Table 1. Frequency of individual plants with stem rust resistant reaction (R) in both of two inoculations, average infection type (AIT), and phenotypic variance (σ_p^2) for AIT for each selection cycle in the forage-type (F) and turf-type (T) tall fescue populations.

		F population			T population		
Selection method	Cycle	R†	AIT score	σ_p^2	R	AIT score	σ_p^2
		%			%		
	C0	5	3.1	1.48	6	3.3	1.10
Polycross (PX)	C1	41	1.5	2.38	45	1.4	2.18
	C2	54	1.1	2.03	50	1.1	2.19
OP-PXr,‡ resistant	C1	18	2.3	2.62	25	2.1	2.62
	C2	63	1.2	1.74	44	0.9	1.89
OP-PXs,‡ susceptible	C2	1	3.2	1.24	5	3.7	0.56
LSD0.05			0.3			0.3	

† Resistant reaction (R) to stem rust was determined for an individual plant by receiving a pustule type score of 0 or 1. Scores were by pustule type on a 0 to 4 scale as follows: 0 = no uredinia or visible symptoms, 1 = small uredinia with necrotic edge, 2 = small to medium uredinia with limited urediospore production, 3 = medium-sized uredinia with moderate sporulation, 4 = large, ragged uredinia with abundant sporulation.
‡ OP-PX, open pollination selection followed by PX selection for resistance (r) or susceptibility (s) to stem rust.

Table 3. Mean panicle length, seed weight, seed yield, and stem rust reaction for populations and cultivars of field grown tall fescue.

Population/cultivar	Cycle	Panicle length†	Weight per seed	Seed yield	Rust severity score†‡	Rust incidence†
		mm	mg	kg ha^{-1}		%
F population, forage-types						
	C0	243	2603	2089	1.9	62
Polycross (PX)	C1	237	2568	2441	1.4	49
	C2	253	2529	2052	1.3	46
OP-PXr,§ resistant	C1	243	2661	2226	1.9	61
	C2	251	2698	2244	1.0	38
OP-PXs,§ susceptible	C2	251	2484	2086	2.0	62
T population, turf-types						
	C0	208	2480	2218	1.8	63
Polycross (PX)	C1	226	2521	2505	1.1	45
	C2	216	2465	2323	1.0	39
OP-PXr, resistant	C1	242	2461	2401	1.6	57
	C2	249	2599	2215	1.0	38
OP-PXs, susceptible	C2	243	2676	2041	2.0	63
Check cultivars						
SSE¶		250	2646	1730	2.3	65
Kentucky 31		228	2520	2274	1.6	55
Arid		232	2447	2032	1.8	62
Mesa		217	2414	2352	1.6	60
Thoroughbred		210	2456	2134	2.1	64
Bonanza		231	2374	2433	2.2	66
Forager		249	3066	2194	2.3	64
LSD0.05		26	119	227	0.3	7

† Stem rust reaction and panicle length from 1997, 1998, and 1999; seed production data included 1996 also.
‡ Scores were on a 0 to 4 scale, based on % leaf area diseased and the pustule type, as follows: 0 = no visible symptoms, 1 = type 1 pustule, <3% of leaf area diseased, 2 = type 2 pustule, <3% of leaf area diseased, 3 = type 3 pustule and <3% of leaf area diseased, or type 2 pustule and >3% leaf area diseased, 4 = type 3 or 4 pustules, and >7% leaf area diseased.
§ OP-PX, open pollination selection followed by PX selection for resistance (r) or susceptibility (s) to stem rust.
¶ SSE = super susceptible check.

demic development and slow evolution in the pathogen, while still providing overall cultivar resistance.

Mean seed yields for four years of production were larger after one cycle of PX selection of the PX group (C1), but not from the PX cycle of the OP group (C2). The F and T populations performed similarly for the other cycles of selection, and there was not a seed yield increase over C0. Reverse selection for susceptibility (OP-PXs) resulted in stem rust reactions and seed yields similar to C0.

The increase in seed yield after one cycle of selection appears to be a heterotic response. With only 14 and 20 original plants in the F and T populations, respectively, heterosis might be expected from an initial PX generation as often occurs in the first generations for synthetic cultivars with a broad genetic base, but few parents. Suggestion of heterosis for seed production, however, was not supported by the panicle length and seed weight data (Table 3).

The correlation coefficient between seed yield and rust severity was -0.46 ($P = 0.05$) and between seed yield and rust incidence was -0.35 ($P = 0.14$) when means of all entries in the test were included, indicating a moderate to low overall negative relationship between stem rust resistance and seed yield. Stem rust infection in tall fescue requires overnight and morning dews, and is favored by warm temperatures (Welty and Barker, 1992). Thus, weather conditions in a particular year greatly affect stem rust development. It was unusual, but there was essentially no stem rust in 1999, and seed yield was highest in that year (Table 4). Stem rust was present the other two years it was measured and a reduction in seed yield from that in 1999 resulted. Rust development may also be affected by weather conditions at different times during plant growth within a year. Rust infection late in the season after panicle extrusion, for example, causes rust to develop on the panicle and florets where it would interfere more directly with seed development. We did not, however, measure stem rust development at different times during the growing season for this study.

The significant entry × year interaction from the ANOVA was demonstrated by comparing populations and cultivars in 1998, a heavy rust year, with 1999, a low or no rust year (Table 5). Stem rust development and seed yields in 1998 followed the direct selection response pattern and the 4-yr average seed yields, but yield patterns in 1999 were much different. In the absence of stem rust pressure in 1999, seed yields among selection cycles were similar, or lower (PX C2 of the F population) than the C0 sources. Commercial cultivars

Table 4. Mean seed yield and stem rust reaction of tall fescue check cultivars in each of four years of seed production.

Year	Seed weight	Seed yield	Rust severity score†	Rust incidence
	mg	kg ha^{-1}		%
1996	2933	2167	–	–
1997	2500	2116	2.3	77
1998	2256	2222	2.7	90
1999	2557	2336	0.0	0
LSD0.05	55	104	0.1	3

† Scores were on a 0 to 4 scale, based on % leaf area diseased and the pustule type, as follows: 0 = no visible symptoms, 1 = type 1 pustule, <3% of leaf area diseased, 2 = type 2 pustule, <3% of leaf area diseased, 3 = type 3 pustule and <3% of leaf area diseased, or type 2 pustule and >3% leaf area diseased, 4 = type 3 or 4 pustules, and >7% leaf area diseased.

Table 5. Mean seed yield and stem rust reaction of tall fescue populations in the 1998 and 1999 seed production years.

Population/cultivar	Cycle	Seed yield		Rust incidence	
		1998	1999	1998	1999
		— kg ha^{-1} —		—— % ——	
F population, forage-types					
	C0	2210	2379	96	0
Polycross (PX)	C1	2848	2430	82	0
	C2	2284	1841	82	0
OP-PXr,† resistant	C1	2261	2433	94	0
	C2	2467	2157	72	0
OP-PXs,† susceptible	C2	1998	2173	99	0
T population, turf-types					
	C0	1914	2223	99	0
Polycross (PX)	C1	2818	2454	76	0
	C2	2663	2228	68	0
OP-PXr, resistant	C1	2577	2288	94	0
	C2	2610	2053	70	0
OP-PXs, susceptible	C2	1364	2348	99	0
Check cultivars					
SSE‡		1719	2268	100	0
Kentucky 31		2245	2623	90	0
Arid		1887	2190	96	0
Mesa		2230	2348	98	0
Thoroughbred		1882	2009	96	0
Bonanza		2172	3333	99	0
Forager		2069	2598	100	0
LSD0.05		634	484	14	0

† OP-PX, open pollination selection followed by PX selection for resistance (r) or susceptibility (s) to stem rust.
‡ SSE = supersusceptible check.

that were bred for high seed yield had high seed yields in 1999, but only Kentucky 31, Bonanza, and Forager were significantly larger than their seed yields in 1998. The SSE that came from cultivars bred for higher seed yields had high seed yield in 1999, similar to other check cultivars, but had significantly lower seed yield in 1998 when it had heavy rust infection. A similar response was found in the reverse selection cycle (OP-PXs) of the T population, but seed yield of OP-PXs of the F population was not significantly different between the 2 yr.

Our results provide evidence that genetic resistance for stem rust in host cultivars can provide high seed yields in years when there is high pressure from stem rust infection. Genetic resistance is a sustainable approach to seed production and incorporation of resistance into tall fescue cultivars could lower the need for pesticides to control the disease. The PX C2 populations provide sources of resistance to stem rust that will be useful in developing improved cultivars. These germplasms were released and designated ORTFRR-T94 for the turf-type population and ORTFRR-F94 for the forage-type (Barker and Welty, 1997).

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